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THE ANTENODAL RETICULATION OF THE WINGS OF AGRIONINE DRAGONFLIES.

BY HERBERT CAMPION.

When describing the remarkable fossil dragonfly *Phenacolestes mirandus*, from Florissant, Prof. T. D. A. Cockerell laid stress upon its possession of five antenodal nervures, and, upon the strength of that character alone, proposed to erect *Phenacolestes*—together with *Dysagrion*, also from the North American Tertiaries—into a new subfamily of Agrionidæ, the Dysagrioninæ.[1] "*Dysagrion* Scudder, the type of the subfamily," he wrote, "has not been supposed to possess an unusual number of antenodals, but it is evidently allied to *Phenacolestes*, which has five; and Scudder's figure of *Dysagrion fredericii* shows two antenodals *beyond* the arculus, and as the first two of all Agrionids must certainly have been present, there were at least four." In the description of *Phenacolestes mirandus* it is stated: "Antenodal sectors five, of which only the first two continue to the radius, these being the two present in Agrioninæ. The second, however, does not meet, or nearly meet, the arculus, but ends on the radius 204μ beyond it (a character also of *Melanagrion*)." On the same occasion Prof. Cockerell described the apical half of a wing, also from the Tertiary of Florissant, as *Phenacolestes parellelus*, but expressed a doubt as to the true generic position of the fossil. Subsequently, he recorded the base of a wing having six antenodal cross-nervures, which he referred provisionally to the same species.[2]

In the typical Agrionine wing we find two antenodals only, which cross transversely both the costal and subcostal spaces; one of them is placed before and the other at the level of the arculus. In fact, so general is this number of antenodals in the Agrioninæ, that for many years it was one of the chief characters used in separating that subfamily from the Calopteryginæ, in which the antenodals are more numerous. In a few recent Agrionines, however, three, or even five, antenodals occur with more or less constancy, and we are therefore no longer able to regard antenodal reticulation as a character of primary importance in the classification of the Zygoptera. Supernumerary antenodals are often weaker than the normal ones, and are frequently incomplete; that is to say, they may appear as short nervures crossing the costal space alone or the subcostal space alone.

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[1] *Bull. Amer. Mus. Nat. Hist.*, XXIV, p. 60 (1908).

[2] *Amer. Journ. Sci.*, XXVI, p. 75 (1908).

As already remarked, the second antenodal coincides with the arculus in the typical Agrioninæ, but in such genera as *Agriocnemis, Argiocnemis, Ceratura,* and *Hemiphlebia,* it comes before the level of the arculus, while it lies beyond it in the fossil genera *Melanagrion* and *Phenacolestes.*

In *Neurolestes trinervis* De Selys, from Kamerun, we get three complete antenodals constantly present, and, according to its describer, the supernumerary nervure is placed between the usual two. *Neuragrion mysticum* Karsch was described from a single ♀ from Ecuador, and here again there is an additional nervure lying between the ordinary ones. But in this case the nervure is confined to the hind-wings and to the subcostal space only. Of *Thaumatoneura,* from Central America, two species are known, namely, *T. inopinata* McLach. and *T. pellucida* Calv. In this genus a fourth, or even a fifth, antenodal is occasionally added to the more usual number of three, and in some instances the number is reduced to two. The third, fourth, and fifth antenodals, when present, are placed beyond the level of the arculus and are confined to the costal space. *Podopteryx roseonotata* De Selys is represented in the British Museum Collection by three specimens, namely, the type ♂, obtained in Aru by A. R. Wallace, and a fine pair (♂ & ♀) from Queensland (F. P. Dodd). The Australian examples do not possess more than two antenodals in any of their wings, but the type specimen has a third antenodal in each wing, beyond the level of the arculus, and crossing the costal space only in three wings, and both the costal and subcostal spaces in the remaining wing. Furthermore, in three wings there is a transverse nervure traversing the subcostal space alone before the first regular antenodal.

Although the South African genus *Chlorolestes* does not normally possess more than two cross-veins before the nodus, there are two specimens in the British Museum Collection which exhibit a third cross-vein. One of these insects is a ♂ of *C. longicauda* Burm., in the right hind-wing of which the additional nervure is placed between the usual two and ceases at the subcosta. The other is a ♂ of *C. fasciata* De Selys, and in this case the added nervure, which ceases at the subcosta, lies before the first normal antenodal in the right hind-wing.

Two Neotropical genera occasionally present similar features to those observed in *Chlorolestes*. The Godman-Salvin Collection of Central American Odonata, now in the British Museum, includes the type and three other specimens of *Paraphlebia quinta* Calv., all from Guatemala. Two of these have an additional antenodal in as many as five out of their eight wings, and in each instance it is proximal to the first regular antenodal and is restricted to the subcostal space. A ♀ of *Heteragrion chrysops* Hag., from Vera Cruz, also in the Godman-Salvin Collection, has, in three of its wings, a supernumerary antenodal between the usual ones and limited to the costal space.

All the recent species which have been considered so far belong to De Selys' Legion Podagrion, a group which has been declared to be "heterogeneous and untenable," but which includes the most archaic genera of Agrioninæ that have yet been made known. However, at least two species belonging to the more highly specialized genera may be cited as affording other instances of the accidental reappearances of the kind under review. One of these is the type ♀ of *Ischnura granti* McLach., from Sokotra, preserved in the British Museum, in which a third antenodal is present in all the wings, except the right fore-wing. In each case it is placed beyond the level of the arculus and ends on the subcosta. The other species referred to is *Pyrrhosoma nymphula* Sulz., concerning which Prof. Philip P. Calvert is kind enough to inform me that he possesses a ♀ from Birmingham, Warwickshire, taken by Mr. W. H. Bath, whose left fore-wing has three antenodals, the third lying beyond the usual two and crossing the costal space only.

It is not improbable that the supernumerary antenodals which we have found to occur sporadically, as an individual peculiarity, represent nervures which were present normally in the wings of some ancestral form, but which have been lost in the majority of living Agrioninæ. The main tendency of Agrionine development has been in the direction of simplified wing-venation, and in the more highly specialized genera the costal and subcostal spaces have shared in the general elimination of superfluous cross-veins. As soon as the number of antenodals had been reduced to two, however, specialization in this direction appears to have ceased, for no Agrionine is known having fewer than two complete cross-veins, except in rare cases of individual aberration. In this connection it will be useful to quote some remarks made by Prof. Calvert respecting two Mexican specimens of *Ischnura denticollis* Burm., which are in the following terms:

"Two abnormalities in venation may be mentioned here: One male from Patzcuaro has only one antecubital on the right hind-wing, situated at the level of the submedian cross-vein. One female from Orizaba has the first antecubital on the right hind-wing only about as far from the second as the costal space is wide, and it crosses only the costal, not the subcostal, space."[3] In consequence of the discontinuous antenodal in the ♀, which I have seen, and the single antenodal in the ♂ lying on the level of the cubito-anal cross-vein in each case, I regard both of them as occupying the intermediate position between the two normal antenodals of Agrioninæ.

If this view should prove to be well-founded, it would follow that we have evidence of the former existence of at least seven antenodals, of which the second and fourth alone persist in the greater number of recent Agrioninæ. In a hypothetical wing, including all the antenodal cross-veins of which indications have so far been afforded by morphology and teratology, the fourth antenodal is that which coincides with the arculus, and this fact enables one to recognize it in all other Agrionine wings. It is also comparatively easy to determine, in any given case, the identity of each of the three antenodals which precede it. But at present I can discover no means of ascertaining the exact homology of the antenodals lying beyond the level of the arculus which occur occasionally in one or two recent genera.

In our reconstructed wing, then, we have seven antenodal cross-veins, disposed in the following manner: Nos. 1, 2, and 3 placed before the level of the arculus; No. 4 coinciding more or less exactly with the arculus, and Nos. 5, 6, and 7 lying between the level of the arculus and the nodus. Arranging in tabular form the material which we have had under review, we get this result:

With antenodals Nos. 2 and 4:
  Agrioninæ (with the exceptions noted below).

With antenodals Nos. 1, 2, and 4:
  Chlorolestes fasciata (teratological ♂).
  Paraphlebia quinta (teratological specimens).

With antenodals Nos. 1, 2, 4, and one other:
  Podopteryx roseonotata (type ♂).

With antenodals Nos. 2, 3, and 4:
  Neurolestes trinervis (teste De Selys).
  Neuragrion mysticum.
  Chlorolestes longicauda (teratological ♂).
  Heteragrion chrysops (teratological ♀).

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[3] *Biol. Centr.-Amer., Neuropt.*, p. 127, footnote (1902).

With antenodal No. 3 only:
  Ischnura denticollis (teratological ♂).

With antenodals Nos. 3 and 4:
  Ischnura denticollis (teratological ♀).

With antenodals Nos. 2, 4, and another:
  Ischnura granti (type ♀).
  Pyrrhosoma nymphula (teratological ♀).
  Thaumatoneura (normally).

With antenodals Nos. 2, 4, and two or three others:
  Thaumatoneura (occasionally).

With antenodals Nos. 2, 4, 5, 6, and 7:
  Phenacolestes mirandus.

Although *Phenacolestes parallelus* is believed to have had six antenodal cross-veins, it has not been possible to place it in the table, as no information has been given concerning the position of the veins in relation to the arculus.

Looking at the number and arrangement of the antenodal nervures alone, and without having regard to any other considerations, it would appear that among recent genera *Thaumatoneura* bears the closest resemblance to *Phenacolestes.* Moreover, this resemblance is accentuated when, as sometimes happens, a fourth, or even a fifth, antenodal is present. But of course the venation of the spaces lying between the nodus and the base of the wing is only one of many characters which must be studied in attempting to arrive at the true affinities of *Phenacolestes*, and for the present it is perhaps advisable to retain in the subfamily Agrioninæ this and other genera associated with it.

In conclusion, I have to thank Professor Calvert for his kindness in suggesting amendments to this paper, and particularly for drawing my attention to the two Mexican specimens of *Ischnura denticollis* recorded by him, and furnishing me with information respecting the British ♀ of *Pyrrhosoma nymphula* contained in his own collection.